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OTOLITH FUNCTIONS AND OPERATING PRINCIPLES
PART I. THE FUNCTIONS OF THE OTOLITHS

Robert Mayne
Manager
Advanced Systems and Technologies Div.

This report is in partial compliance to a contract under the
National Aeronautics and Space Administration
Manned Spacecraft Center
Gemini Flight Support Procurement Section
Houston, Texas
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SUMMARY

A series of three reports are planned in the development of a theory of "Otolith Functions and Operating Principles." These reports will include:

Part I The Functions of the Otolith Organs

This report will discuss what functions the otoliths are believed to fulfill on the basis of experimental data reported in the literature and some qualitative tests.

Part II The Mechanics of the Otolith Organs

This report will develop a proposed mechanical model of the otolith sense organs and discuss the synergetic interaction between semicircular canals and otoliths in cancelling out the effect of gravitation during a turn of the head. It will discuss, also, the synergetic interaction between eye movements and otolith signals.

Part III Interpretation of Single Fiber Activity

This report will review the literature and experimental data on single fiber activity and will develop a mathematical interpretation of data by Lowenstein and Roberts[23] on the activity of fibers during rotation of a fish preparation. The analysis will be shown to be in harmony with the proposed model.

OUTLINE

PART I. THE FUNCTIONS OF THE OTOLITHS

INTRODUCTION

BASIC OTOLITH FUNCTIONS
as judged from experimental data published
in the literature

DETERMINATION OF THE DIRECTION OF INERTIAL FORCES

Acceleration and Gravitation

The Oculogravic Illusion

The Perceptual Priority of Sensory Data

DETERMINATION OF THE MAGNITUDE OF INERTIAL FORCES

Counterrolling of the Eyes

Resolution of Forces

Long Time Integration of Otolith Signals

DETERMINATION OF VELOCITY

Oscillation in a Parallel Swing

Qualitative Tests

Movements of Small Amplitude

Movements of Large Amplitude

CONCLUSIONS

INTRODUCTION

The theory of the otolith functions and of their operating principles has not progressed to the same stage as that of the semicircular canals. The approach still lacks the equivalent of Steinhausen's [39] contribution in the way of the demonstration of the movement of the cupula and the expression of the canal response by a differential equation. This simple concept made possible much of the extensive experimentation on semicircular canals and provided a high degree of predictability in related phenomena. The present set of reports attempts to set forth a theory of the basic operating principles of the otoliths in the hope that it may lead to similar advances in the linear portion of the vestibular system.

It was natural for early investigators, such as Breuer, to expect that the otoliths would be organized to measure movements about three perpendicular linear axes. The findings that fish and birds possessed three otolith organs seemed to confirm this view and, by symmetry with the configuration of the semicircular canals, to indicate that each of these organs would be associated with movements along one of the three linear axes with respect to the head. The fact that mammals possess only two otolith organs presented some difficulty to this point of view, but the problem had to be set aside in the hope of future solution. Later experimental work, as by Adrian[1] and Lowenstein, et al,[23] forced abandonment of this concept by showing that the firing rate of fibers issuing from the same macula is associated with movements or forces along different axes.

These recordings demonstrated another significant point. A change of orientation of a preparation with respect to gravity produces both transient and static changes in the firing rate. The significance of these transient "change of position signals" was probably not fully appreciated at the time. Guedry and Harris[17] pointed out that they were indicative of a velocity measurement by the otoliths. They argued that a change in the force of gravity on the otoliths should be the equivalent of a change of acceleration, a necessary requirement for the generation of a measurable velocity.

At the same time, the evidence is clear that the otoliths respond statically to constant acceleration, or a constant gravitational force. A clear concept of the mechanism permitting the otoliths to fulfill this dual role is lacking. This report attempts to describe such a mechanism.

Further experiments and theoretical elaborations are needed to check the validity of the proposed otolith model. Some changes may have to be made to provide a better fit to new experimental data. The model, however, seems to fit a large body of available experimental data and it is hoped that it may stand in its more general outline, or at least that it may provide a significant step toward the understanding of this complex and intriguing biological system.

It goes without saying that any speculation on the likely effect of weightlessness on orientation and the devising of critical experiments to investigate such effects must rest on a reasonably well-established working hypothesis of the functions and operating mechanism of the otolith organs. It is hoped that the present report may be a contribution to this basic goal of vestibular studies by NASA.

BASIC OTOLITH FUNCTIONS

This report will first review briefly some of the experimental evidence regarding what modalities of motion are detected by the otolith, and what purpose otolith sensory data may serve in the control of body movements.

DETERMINATION OF THE DIRECTION OF INERTIAL FORCES

Acceleration and Gravitation

Man and animals are subjected to a constant gravitational field of force on the surface of the earth. This force is the equivalent of one caused by an acceleration of 32 feet/second^2 directed radially away from the center of the earth. Insofar as stresses on the body are concerned, gravitational forces are indistinguishable from accelerational forces. Both forces are proportional to mass and may be referred to as "inertial forces." Only accelerational forces, however, can be related to motion with respect to the earth. Any movement-detecting system based on the measurement of acceleration must separate these two forces. This is the most difficult requirement in the design of an inertial navigation system such as used on guided missiles. The manner in which the vestibular system performs this separation will be discussed later in the report. It should be obvious at this point, however, that the cancellation of gravitation can only be accomplished if its magnitude and direction are known. In an earth environment where gravitation is constant, this amounts to knowing the direction of the vertical.

The direction of the vertical must be known for other reasons, as for the maintenance of posture and body equilibrium. Small changes of attitude of the body with respect to the vertical must be promptly reported to the central nervous system (CNS) for appropriate compensatory action. The organization and programming of complex body movements as in a leap, a somersault, or in the mere act of walking, must take the direction of the vertical into account as the compensation of gravitational forces represents a large portion of the effort which must be exerted in carrying out these movements. The computations which are performed in setting up the appropriate programs must start with a knowledge of the direction and magnitude of these forces.

As discussed in an earlier report,[26] this information is carried in the system of spatial representation where a record of features of the environment are organized about three main axes: the vertical, the horizontal, and a major longitudinal axis. The information is continually up-dated on the basis of various sensory data, mainly the eyes, and vestibular signals. The otoliths, operating synergetically with other senses, supply data about the direction of the vertical, while the semicircular canals appear to be mainly effective in supplying data about a change of orientation of the body.

In order to perform their functions, the otoliths must measure linear acceleration. They differ in this respect from the semicircular canals, which, as indicated earlier,[27] measure only transient angular velocity for normal body movements. While angular acceleration is the stimulus to the canals, its value is lost in the hydromechanical integration they perform. It is possible, however, that the value of acceleration may be recovered by an inverse operation or a differentiation of vestibular signals. We will consider briefly some of the evidence that the otoliths measure linear acceleration.

The Oculogravic Illusion

If an observer in a seated or erect position is subjected to a linear acceleration normal to the longitudinal axis of his body, the force he experiences is the resultant, in both direction and magnitude, of this acceleration and of gravitation. It is found that he will then estimate the direction of the vertical to coincide closely with the resultant force. This phenomenon has been called the oculogravic illusion.[3,4,5,6,13,14,15]

Clark and Graybiel[6] investigated the part played by the otoliths in this illusion. They tested both normal and labyrinthine defective (LD) subjects in a centrifuge. Centripetal acceleration and gravitation combine under these conditions in a resultant which is inclined with respect to the true vertical. They found that both normal and LD subjects perceived the change of direction of the force as an illusory change in the direction of the vertical, but normal subjects estimated the amount of change much more accurately. In another series of tests, Graybiel and Patterson determined the threshold in the detection of a small change of direction of the resultant acceleration for normal and LD subjects. The tests showed a lower threshold and a more consistent perception for normal subjects, although there was some overlap with LD subjects. There was no adaptation to the perceived direction of the vertical following a certain period of adjustment to the new direction. It is significant to note in both cases the performance was improved by practice.

It can be concluded from this series of tests that the otoliths and body sensors both provide data about the direction of combined acceleration and gravitation. The otoliths, however, provide more accurate data and have a greater resolution. The superiority of the otoliths appears more marked in the actual measurement of the direction of the resultant than in their threshold. The fact that the threshold for a change in direction of inertial forces could be improved by practice in the case of both LD and normal subjects is believed to indicate, as discussed below, that neither of these two sets of sensory data is by itself the principal factor in the detection of a change of body orientation during normal body activity. The LD subject depends, presumably, mainly on vision, while the normal subject is believed to depend on synergetic visual and vestibular reactions. It must be said, also, that in normal life situations with relatively rapid movements, the otolith signal, as indicated later, is much greater than in the case of slow changes resulting from an increase or reduction of the speed of a centrifuge. The rate at which a change of orientation of inertial force is effected should be controlled in threshold experiments.

The Perceptual Priority of Sensory Data

Clark and Graybiel reported that when normal subjects experience a change in the speed of the centrifuge and a corresponding change in the direction of the resultant force exerted on their bodies, they perceive the direction of the vertical to rotate gradually from the original position to a new one coinciding closely with the actual direction of the resultant force. They called this part of the illusion "the dynamic phase." LD subjects experienced this phase to a lesser degree, and, as indicated above, grossly underestimated the amount of change. The explanation of this dynamic phase probably rests in the manner in which sensory data are organized, and the long integration time required for otolith signals in the determination of the vertical.

It may be stated as a law of sensory organization that when redundant sensory data are available about a given stimulus, the sensory data with the greatest information content for a given change of stimulus will be utilized by perception. It is interesting to speculate whether this law could account for Witkin's[46] observation that the personality of a person influences what cues he utilizes in determining the direction of the vertical. It could be that causes and effects are inverted and that personality is influenced by the resolution of our various senses. But this is not the place to pursue such speculations.

The driver of a car, for instance, has many cues he could utilize in his driving. He might utilize his visually detected position with respect to a white line, or the perceived distance from a preceding car. The choice is made unconsciously and depends upon which data provide the better information, and this may vary in turn with road conditions, speed of traffic, and the state of mind of the driver. Following the selection of a specific clue, alarm reactions must be set up to warn of changed conditions. When these fail, a driver may follow the lead car as it pulls into a gasoline station and crash into its rear. Many such accidents have been reported.

When the body is inclined with respect to gravity as a result of a normal body movement, a number of cues are provided by various sensors, including mainly those of vision, body reactions, semicircular canals, and otoliths. If the semicircular canals have a greater information content (a greater number of just noticeable differences (j.n.d.)] for the change, body control will be organized to respond to their signals and will disregard others. Actually, as discussed later, it is believed that changes in orientation of the body are best detected by synergetic action between the vestibule and the eyes. Without vision, however, it would appear that the semicircular canals are next in line. When the direction of inertial forces on the body is changed without rotation, perception must resolve a conflict. The lack of semicircular canal signals is taken to signify "no turn," while body reactions and otolith signals mean "a turn." The no turn meaning is given considerable weight on the basis of past adaptation and takes time to dissipate. At the same time, as indicated below, otolith data in the determination of the vertical must be averaged up over a long period of time before they give accurate information. The result is a perception of a gradually changing orientation marking the decay or dissipation of the perceptual interpretation of "no semicircular signal." There is no such delay when the change of orientation of the body with respect to gravity is accomplished by rotating a subject seated in a chair because of adequate semicircular canal signals. Passey and Guedry[37] found that when subjects are rotated in a chair to a position other than the vertical, they can right themselves more accurately immediately after the turn than a period of time later. This may be taken as evidence of adaptation but could be, also, the result of dissipation of the cues from the semicircular canals. This observation seems to be further evidence of the priority assigned by perception to the semicircular canal information in the detection of a rapid change of body orientation.

Another set of experiments by Guedry and Harris illustrates the principle of sensory organization. In this experiment, normal and labyrinthine defective subjects were oscillated in a parallel swing while lying down, face up, with the axis of the body perpendicular to the motion. The normal subjects sensed the actual motion quite accurately although with some overestimation of its amplitude. The LD subjects sensed mainly an angular oscillation of the body accompanied sometimes with sideways displacement.

Subjects in a parallel swing move along the arc of a circle about a center half way between the two suspension points of the swing. During a full oscillation the direction of resultant inertial forces with respect to the body is continually altered and must remain parallel to the suspension wires as these can only take tension forces without shear. The body, however, experiences no rotation and the normal subjects receive no signal from the semicircular canals. Because of non-operative vestibule, previous adaptation has not led LD subjects to associate a turn with semicircular canal sensory signals. The lack of signals during oscillation does not carry, therefore, the perceptual meaning of "no turn" which it carries in the case of a normal subject. The meaning of body cues is, therefore, more readily accepted. Without vision, body cues are next in line for the LD subject in signifying rotation. The result is that the LD subjects perceive the change of direction of forces on the body and interpret it as a rotation of the body. The linear acceleration forces experienced on the body may or may not be integrated into a perception of velocity, and the LD subject may or may not perceive linear displacement. If he does, it will be of very much lower amplitude than the actual movement. The combination of linear oscillation and body rotation will then be interpreted as an oscillation in an arc of circle about a center below the subject as the simplest motion which fits sensory data.

The previous discussion emphasizes the need of care in experimental procedure to distinguish between the reaction of naive and sophisticated subjects. If a naive subject responds immediately to an experimental stimulus, it is because the stimulus corresponds to a life situation and that the response has been adapted to it. If his performance can be improved radically by practice, it is because sensory data previously ignored because of low perceptual priority are being adapted to the new task. If little or no improvement results from practice, it is because no sensory data are available. The evidence presented above is to the effect that otolith signals, by themselves, have a relatively low priority in the determination of a change of direction of the inertial forces with respect to the body, but are effective in the determination of the vertical over a long integrating period.

DETERMINATION OF THE MAGNITUDE OF INERTIAL FORCES

Counterrolling of the Eyes

It has long been known that whenever the head is inclined toward a shoulder with the body erect, the eyes will roll in the opposite direction. Woellner and Graybiel[48] measured counterrolling as a function of the amount of centrifugal force acting laterally on the body. Miller[32] measured counterrolling as a function of the lateral inclination of the head and body. The two sets of data are in general agreement to the effect that counterrolling is approximately proportional to the component of inertial force acting laterally on the head. These observations demonstrate that sensory data related to the magnitude of inertial forces acting laterally on the head are available to the system of body control. Further experiments by Miller and Graybiel[31] demonstrate that this data is of vestibular origin. They showed that the amount of counterrolling exhibited by LD subjects was very much less than observed with normal subjects. The measurements of counterrolling, however, were made under static conditions. It is believed that under dynamic situations following a rapid change of lateral acceleration, the movement would be greater at first before reducing to a static value, and, therefore, would include both a transient and a static component. As the case may be, the above observations show that the otoliths provide information regarding the magnitude as well as the direction of inertial forces.

Resolution of Forces

Actually, the determination of direction cannot be separated from the determination of amplitude. Direction can only be determined by measuring the magnitude of the component forces about three axes and combining these forces into a resultant. It is true, however, that we sense direction as separate from magnitude and as long as we are in a normal earth environment we only need to establish the direction of the vertical since the value of gravitation is constant. Any detectable change in this magnitude would be interpreted without other data as meaning acceleration and movement, as is the case in an elevator. Subjects, however, become adapted to a centrifuge and learn to interpret properly the increase of the force they experience. They do not feel they are flying along a spiral path at a constantly increasing velocity.

It is interesting to note that the direction of the vertical cannot be determined accurately by a subject in the prone or inverted position without visual clues. This may be attributed to inaccuracies in the determination of the component of force on the longitudinal axis of the body. The longitudinal accelerometer experiences a variation of 2g between normal and inverted position and this may well exceed its operational limits. The velocity portion of the otolith transducer to be discussed later must also saturate rapidly when subjected to a constant acceleration.

Long Time Integration of Otolith Signals

The measurement of the magnitude of the components of acceleration along the three body axes make it possible to compute the direction of the resultant inertial force on the body. This direction, however, does not represent the true vertical at any specific moment because of the disturbing effect of a possible acceleration. If the signals are integrated over a long period, however, the transient accelerations to the right or left, forward or backward, cancel out and they determine the true vertical. Sudden changes can then be detected by the semicircular canals, or by visual observations modified by involuntary eye movements controlled by vestibular signals. We have seen before an example of the slow determination of the vertical when semicircular canals and visual cues are missing. In a similar way the vertical in a navigational system such as used in an airplane is determined by applying light precessing torques on a gyroscope as a function of accelerometer signals. The gyroscope then can detect any rapid departure of the vehicle from the vertical. Lowenstein[22] reports that when the utriculus of fish are destroyed, they exhibit an oscillation and a tendency to over-compensate for angular acceleration. A navigation system which had lost the erection of the gyroscope would operate in a similar way. There would be righting functions as a response to the rate of turn, but they would tend to diverge from the vertical. Oscillations would result if the navigation system had other means as the fish probably has, of determining the vertical, but these substituted means had a much higher threshold and less constancy than the normal ones.

DETERMINATION OF VELOCITY

Functional considerations would suggest that the control of body movements requires the same information about linear velocity and extent of linear motion that the semicircular canals supply about angular movements. Considerable evidence is to be found in the literature that such is the case. If so, the otoliths must perform a dual role in the measurement of acceleration and velocity. Evidence that such is the case is to be found in the literature.

Oscillation in a Parallel Swing

Walsh[44] reported that for oscillations in the direction of the long axis of the body, the sensation of motion leads the actual motion for periods of ten seconds, or for a frequency of 0.1 cps, but is nearly in phase for periods of one to two seconds, or for frequencies of 1 to 0.5 cps. If we identify sensation of motion with sensation of velocity, this observation would indicate that linear velocity is measured by an overdamped oscillatory system similar to the semicircular canals in the measurement of angular velocity. A frequency of 0.1 cps would then be below the normal frequency response of the system, while 0.5 to 1 cps would be within it. Sensations, however, may not be a true guide of the response of the velocity transducer because of the shift of sensed body position, as discussed in a previous report. The fact that normal subjects in the Guedry and Harris experiments with a parallel swing perceived their approximate true motion in an arc of a circle with the center above them is most readily explained by the detection of velocity about two body axes and the determination of the resultant velocity and displacement in the CNS.

Correia and Guedry[7] observed the phase shift relationship between the displacement of a swing and ocular motion for labyrinthine defective and normal subjects under different instructions. The instructions included: eyes closed relaxed (ECR), eyes closed fixated (ECF), eyes open fixated (EOF), and counter-displacement (CD). Their data for one subject are reproduced in Figure 1. The subjects were encapsulated in a hood and had no visual contacts with the environment. It will be noted that for the ECR condition, the response is in phase with acceleration. The response may be due to the acceleration transducers. The other three responses appear to be similar, judging from the nomenclature in the figure. If we assume, however, that the response corresponds mainly to an attempt to fixate the ceiling, we can determine the accuracy of the motion if we know its distance. Doctor Guedry advised in private correspondence that the height of the ceiling over the subject was nine feet. If, then, we assume that the subject has a memory of this distance and that the data on Figure 1 corresponds to his attempt to fixate a point on the ceiling half way between the wire attachments, we can determine from the geometry of the situation what degree of success he is achieving. Figure 2 illustrates the actual eye movement compared to the ideal movement required to provide fixation on the ceiling half way between the two suspension points. The theoretical curve was plotted on the basis of an over-estimation of the amplitude of motion by a factor of 1.4 corresponding to that observed by Guedry and Harris. It will be noted that fixation is provided to a close approximation. The motion of the eyes is of a type observed in body movements in response to a random input, where the movement is corrected whenever the error exceeds a certain threshold.[28] The eye movements appear, therefore, to be controlled on the basis of body position rather than velocity as is the case for angular

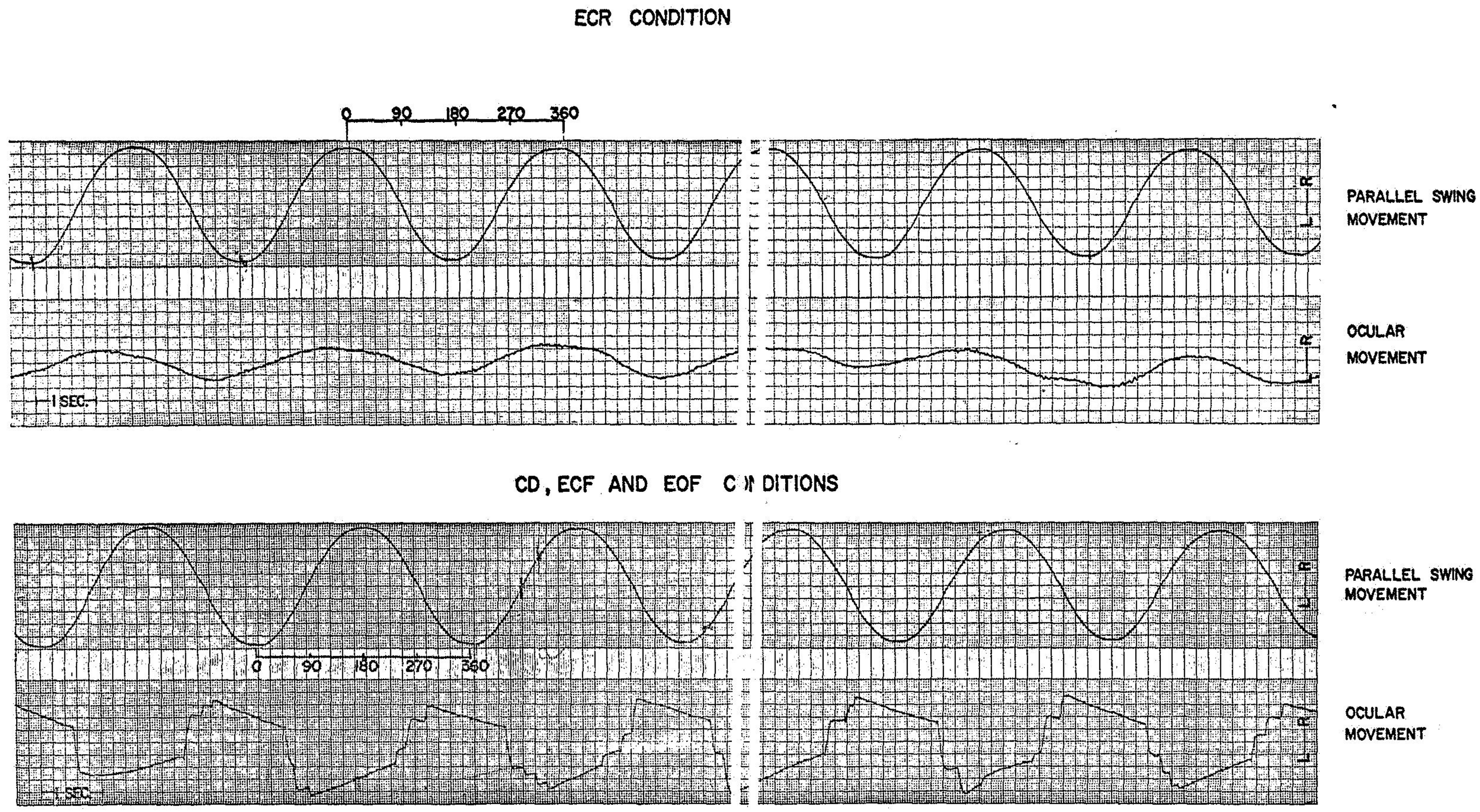

Figure 1

Recordings of Parallel Swing Movement and Ocular Movement for a Normal Subject under the Condition of Eyes Closed Relaxed and under Conditions Where Subjects were Instructed to Counterdisplace the Eyes (ECF, EOF, and CD Conditions)

Reproduced from <u>Phase Relations between Sinusoidal Ocular Displacement and Parallel Swing Displacement in Normal and Labyrinthine-defective Subjects</u>, by M. J. Correia and F. E. Guedry, USN SAM/NASA Joint Report No. 92, Project MR005.13-6001, 10 January 1964.

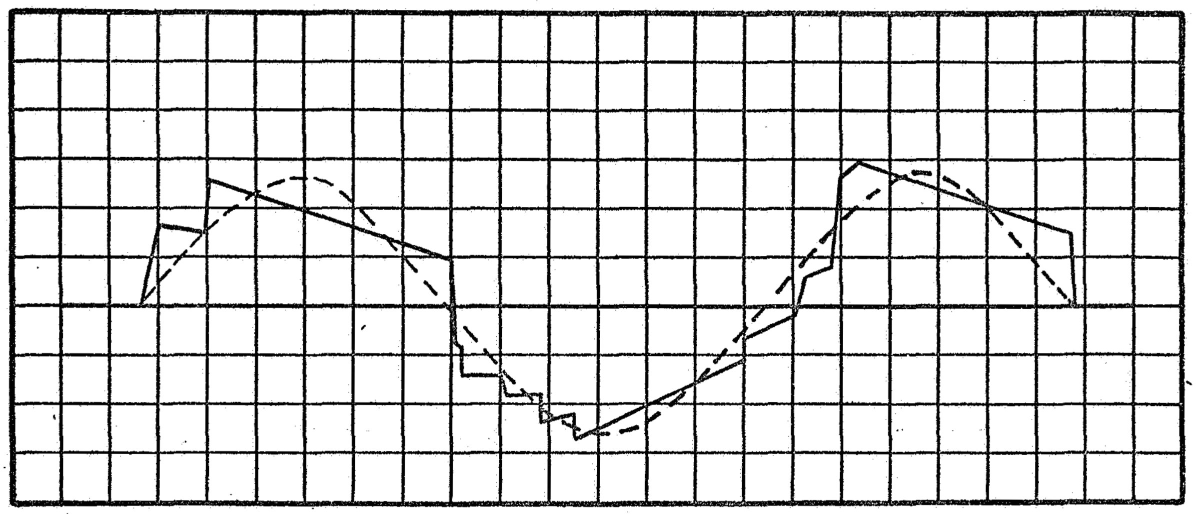

Figure 2. Actual eye movement and ideal movement to produce fixation on ceiling half way between suspension points. (Actual eye movement taken from Figure 1.)

——— Actual movement
----- Ideal movement

motion of the head. The different modes of control appear to be dictated by the different geometry of the two cases. The data of Correia and Guedry indicate rather clearly that body position is established by means of vestibular data. While normal subjects showed a rather consistent phase shift of eye movements with respect to swing oscillations, L D subjects exhibited a nearly random phase shift. This observation, combined with that of Guedry and Harris[18] that normal subjects estimated the amount of displacement of the swing with much greater consistency and accuracy than LD subjects, appears very strong evidence that otoliths supply the necessary data to establish body position.

It must be emphasized that providing fixation during a linear movement calls for much more complex computations than during an angular movement. In the latter case, it is enough to rotate the eyes with respect to the skull at the same speed as the rotation of the head and in the opposite direction regardless of the distance of the object. In the case of a linear movement, the position of the body must be established with respect to the memorized fixation point by means of data supplied by two linear transducers. A different angular position of the eyes with respect to the head must then be computed for each position. It is rather remarkable that so high a degree of accuracy could be achieved under the test conditions. The data indicates a high degree of awareness of spatial relations between body and point of fixation.

It would appear that nystagmus in the case of linear movement would be of value only in the case of the survey of a field of view at a very short distance so that substantial changes of angle of sight would occur during the movement. It may be useful, also, while traveling in an automobile at relatively high speed and surveying a scene at a close distance. The sense of velocity in this case, however, would not be obtained from the vestibule. Doctor Guedry advised this contractor that some nystagmus was obtained in the swing experiment, but was not reported, probably because of lack of consistent response.

It would be interesting to attempt to condition subjects to generate nystagmus by linear oscillation and a suitable field of view. Such experiments, if repeated in the dark, would provide further evidence regarding the availability of velocity and displacement data from the otoliths.

Qualitative Tests

A few tests were conducted by this contractor in an attempt to verify the conclusions that the otoliths supply data which are utilized to determine body position. The tests were purely qualitative and were performed on six subjects, including a female secretary and five members of the engineering staff. Subjects were seated in a chair placed on a smooth running cart equipped with rubber tires.

Movements of Small Amplitude

The tests were performed by moving the cart by hand. The subjects were asked to look at an object on a table, touch it with a finger, then close their eyes and touch it again after being moved by six to eighteen inches. The qualitative results of this experiment were mixed. Some subjects performed the task quite well with good accuracy. Others did not do as well, but their performance improved definitely with practice. Practice meant that the subjects merely kept their eyes open and touched the object while being moved back and forth. Three of the subjects reported an interesting reaction. Upon being moved from one point to another over a distance averaging one foot, and therefore being first accelerated and then decelerated, they experienced the sensation of being first moved by the approximate correct distance, then returned to their original positions. Practice seemed to reduce or eliminate this illusion.

It was pointed out in a previous report that an integrating accelerometer of the overdamped oscillatory type gives a signal corresponding to this sensation. In the case of a rotary movement from one position to another, it was shown that the semicircular canals similarly signal a return to the original position. It was speculated that this returning illusion was eliminated by proper compensatory reactions developed as the result of normal body activity. It could be, therefore, that for some reason, perhaps related to synergetic eye movements, the compensatory reaction does not develop in the case of linear movements. The phenomenon merits further investigations as its true, verified, explanation would no doubt throw considerable light on the mechanics of otolith organs and adaptation to their signals. The tentative conclusions of the tests, however, are that man maintains spatial representation without visual contact with his surroundings while being moved linearly for short distances. This representation is presumably achieved by means of otolith sensors.

Movements of Large Amplitude

If we look at a point in a room, such as the corner of a desk, at a distance of, say, ten to fifteen feet, we find that we can close our eyes, walk to it, and touch it with fair accuracy. The question arises as to what sensual data are used in the performance of this task. Do we count our steps, or is the information of vestibular origin. Some experiments were devised to test these two possibilities.

Subjects were again seated in the rubber tired cart. A large hall was used for the test. The subjects were asked to pick a point about ten to twenty feet away, then close their eyes. The cart was then started as smoothly as possible. The task of the subject was then to signal the time of passing the selected point. Reasonable accuracy was achieved of the same order of magnitude as by walking. It appears, therefore, that in normal body activity we utilize vestibular data in the control of body movements.

In another test the cart was moved at a constant speed with the subject keeping his eyes opened for a distance of some 75 feet and about 20 to 30 seconds. He would then close his eyes while selecting a point some fifteen or twenty feet ahead and then would attempt to signal the time of passing the selected point. Similar accuracy was achieved in this test as in the preceding one.

The tests seem to indicate that otolith signals can supply data on linear velocity, but that velocity can also be obtained visually. It could be that in either case velocity information is stored in the CNS and that computation for displacement takes place at this level. Such an arrangement would have the advantage of providing a much larger integration period than would be possible in any likely otolith mechanism. In contrast, the sensation of angular velocity appears to be closely related to semicircular characteristics and decays at a rate predictable on the basis of their mechanism. The difference in requirements may lie in the fact that we are likely to maintain a constant linear velocity for much longer periods than angular velocity, and, therefore, long integration periods are required for estimation of linear motion. Normal angular movements are of short amplitude and duration and proper integration can be provided by the semicircular canals alone. It is likely, however, that the otoliths operate in a manner similar to the semicircular canals for short transient movements without CNS storage of velocity information. The fact that we can estimate the change of position of a car in heavy traffic when traveling at a constant velocity reflects on the ability of the system of spatial representation to operate over long integration periods, longer than possible with conceivable otolith mechanisms.

Obviously, more controlled tests are needed to investigate otolith response to linear movement. The least that can be said about the qualitative tests run by this contractor is that they do not contradict previous conclusions about the capacity of the otoliths to provide velocity information. Actually, it seems they add weight to these conclusions.

CONCLUSIONS

The evidence presented above indicates that the otoliths fulfill a function in the determination of the vertical through a long time averaging process, that they provide velocity information for short transient linear movements, and supply the system of spatial representation with data about any change of velocity for longer integration periods in the CNS. It will be shown later that the otoliths operate, also, to control eye movements.

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